TRIBES AND GENERA OF THE CINCHONEAE COMPLEX (RUBIACEAE)[1]

Lennart Andersson[2]

ABSTRACT

The phylogenetic relationships of taxa recently referred to the tribes Calycophylleae, Cinchoneae, and Hillieae were analyzed using cladistic methods. The analyses used morphological and micromorphological characters, and a selection of 60 species were used as terminal taxa. It was concluded that all three tribes are supported as monophyletic but must be altered somewhat in circumscription. The tribes Cinchoneae and Hillieae are sister groups, and these two in turn form the sister group of the Calycophylleae. The tribe Calycophylleae should comprise the genera *Alseis*, *Calycophyllum*, *Capirona*, *Ferdinandusa*, *Macrocnemum*, *Wittmackanthus*, and the new genus *Semaphyllanthe* L. Andersson here segregated from *Calycophyllum*. These genera are all supported as monophyletic, although the support is sometimes weak. The tribe Hillieae should comprise *Balmea*, *Blepharidium*, *Cosmibuena*, and *Hillia*. It was not tested whether or not these genera are monophyletic. The tribe Cinchoneae should comprise *Cinchona*, *Joosia*, *Ladenbergia*, *Maguireocharis*, *Pimentelia*, *Remijia*, *Stilpnophyllum*, and the new genus *Cinchonopsis* L. Andersson here erected for *Cinchona amazonica*. *Dolicholobium* occurs as a basal clade of the Cinchoneae but its position is unstable and it is possibly not related to this alliance at all. *Cinchona* is supported as monophyletic if *C. amazonica* and *C. henleana* are excluded, the latter one being transferred to *Ladenbergia*. *Ladenbergia* is supported as monophyletic in approximately the traditional sense. *Remijia* is supported as monophyletic if *Cephalodendron* is included. *Joosia* and *Stilpnophyllum* are supported as monophyletic, while the remaining genera are monotypic. Six new combinations are made: *Semaphyllanthe intonsa* (Steyerm.) L. Andersson, *S. megistocaula* (K. Krause) L. Andersson, *S. merumensis* (Steyerm.) L. Andersson, *S. obovata* (Ducke) L. Andersson, *S. spectabilis* (Steyerm.) L. Andersson, *S. venezuelensis* (Steyerm.) L. Andersson, and *Cinchonopsis amazonica* (Standley) L. Andersson.

The tribe Cinchoneae is often widely circumscribed (see, e.g., de Candolle, 1830; Schumann, 1891, 1897; Robbrecht, 1988). In this sense it is a pantropical group comprising all genera with multiovulate ovaries, ascendingly imbricate ovules, and winged seeds. The case was examined by Andersson & Persson (1991), who concluded that a number of genera traditionally included in the Cinchoneae are not at all closely related to *Cinchona*. Out of 50 genera referred to the Cinchoneae by Robbrecht (1988), 10 were transferred to the Hedyotideae and six to the Condamineae. Disregarding four genera left as incertae sedis, the remainder were divided among four tribes. The paleotropical genera, except *Dolicholobium*, were referred to the tribe Coptosapelteae. Four genera, *Alseis*, *Calycophyllum*, *Schizocalyx*, and *Wittmackanthus*, were referred to the new tribe Calycophylleae. *Hillia* was left in a monotypic tribe of its own, the Hillieae. Thirteen genera were left in the Cinchoneae: *Capirona*, *Cephalodendron*, *Cinchona*, *Cosmibuena*, *Dolicholobium*, *Ferdinandusa*, *Joosia*, *Ladenbergia*, *Macrocnemum*, *Maguireocharis*, *Pimentelia*, *Remijia*, and *Stilpnophyl-*

lum. The relationships between these four tribes were not resolved in strict consensus although a majority of equally parsimonious solutions suggested that the Coptosapelteae are possibly the sister group of the three neotropical tribes, which in turn may form a monophyletic group. The tribes Cinchoneae and Hillieae are probably sister groups, forming together the sister group of the Calycophylleae.

The investigation of Andersson and Persson was based in large part on data from the literature, using genera as terminal taxa. The aim of the present study is to reach higher resolution regarding circumscription and interrelationships of the neotropical tribes and genera of the Cinchoneae complex, using original observations throughout and species as terminal taxa.

Two initial assumptions are based on the findings of Andersson & Persson: (1) the neotropical tribes Calycophylleae, Cinchoneae, and Hillieae form a monophyletic group, possibly including also the genera *Balmea* and *Blepharidium*; (2) the sister group of this complex is the tribe Coptosapelteae. Neither of these assumptions was fully supported,

but they are accepted here in lack of a better hypothesis.

The genus *Schizocalyx* was included in the Calycophylleae by Andersson & Persson but, the fruit and seed characters now having been examined, it appears that its closest relative is *Bathysa* in the Rondeletieae. It is therefore excluded from this study.

MATERIALS AND METHODS

Observations of morphological features were made on herbarium material, occasionally supplemented by pickled material. Species descriptions were used as a basis for coding and were based on numerous collections; a list of representative material studied is given in Appendix 1. Most vegetative characters were observed on dry material, supplemented by label data. Vegetative buds, flowers, and seeds were boiled in water before dissection and observation.

Leaf blade anatomy was observed in material cut by hand from boiled leaves and examined under the interference contrast microscope without staining.

Observations on the sculpturing of the inside of exotesta cells were made with the aid of the scanning electron microscope (SEM), using material treated in the following way. Rehydrated seeds were stored in 70% ethanol and transferred to tap water before treatment. The outer exotesta wall was oxidized by treatment in 15% HNO_3 on a boiling water bath for 5 min. The seeds were then rinsed twice in distilled water and treated with a sonicator at 8 microns. No treatment time was found that suited all materials, and a series of treatments varying between 1 and 20 seconds was therefore tried for each sample. After sonication the seeds were rinsed in water, transferred briefly to 96% ethanol, and left to dry on a slide. Generally, only one seed sample from each species was studied.

Pollen characters were studied with the aid of the SEM, using the methods described by Andersson (1993). Generally, only one sample per species was studied.

The cladistic analyses were performed using the PAUP software package (Swofford, 1993). Numerous preliminary runs were made to guide the selection of taxa and characters as well as the coding of characters. The final runs, on which the following discussion is based, were divided into two steps.

Step I was designed to reveal major subdivisions in the complex, i.e., mainly aiming at establishing tribal delimitations. For this a matrix was used comprising a small number of representatives (Fig. 1) from all "generic level" groups found in the preliminary runs. In this first series *Hymenodictyon floribundum* was used as outgroup, being a taxon mostly included in the Coptosapelteae in the investigation by Andersson & Persson (1991), and one for which a complete data set was available. Four characters were deleted in Step I: 2, 43, 47, and 57.

Step II was designed to achieve better resolution and a more detailed hypothesis concerning the "*Cinchona* clade," clade 60 of Figure 1. For this purpose a matrix was used containing ca. 10 species each of the larger genera and all species of the smaller genera for which sufficient data were available (Fig. 2). Two species found in Step I to belong to basal clades of the sister group were used as a joint outgroup, *Ferdinandusa elliptica* and *Macrocnemum roseum*. Thirteen characters were deleted in Step II: 13, 14, 16, 29, 31, 32, 33, 35, 39, 46, 56, 59, and 60.

The 60 terminal taxa were selected arbitrarily from ca. 120 species actually investigated in order to minimize the amount of missing data.

The selection of characters was based on experience from an ongoing species level revision, and all recorded characters found to vary among species and being shared by at least two species were included in preliminary runs. Characters found in preliminary runs to be highly homoplasious were then excluded. All characters and states are listed in Table 1.

PAUP was run with the following optional heuristic search settings: addition sequence = simple, 1 tree held at each step, TBR branch swapping performed, MULPARS option in effect, steepest descent option not in effect, MAXTREES = 1000, multistate taxa interpreted as polymorphism. Quantitative characters (4, 11, 27, 30, 48, 58) were treated as ordered, others as unordered. After a first run with unweighted characters, the characters were reweighted by the maximum value of the rescaled consistency index. Successive reweighting was then performed until reaching a constant number of trees and identical consensus trees in two successive runs. In step two, monophyly of the outgroup was secured by reinforcing a monophyly constraint tree.

A complete character matrix is given in Table 2; also included in this table is a list of acronyms with corresponding species names and authorities. The results of the cladistic analyses were analyzed with the aid of the MacClade package (Maddison

Figure 1. Trees from the Step I analyses.—A. One out of nine equally parsimonious minimal trees resulting after successive reweighting. Figures on edges are ordinal numbers used in the discussion and the apomorphy list.—B. Strict consensus of the 24 minimal trees resulting from the search based on equally weighted characters.—C. Strict consensus of the 9 minimal trees resulting after successive reweighting. Zero length edges are collapsed. Acronyms are explained in the legend of Table 2. A complete list of apomorphies of tree A is provided in Appendix 2.

& Maddison, 1992), which was also used for numbering of edges of the trees presented here.

THE CHARACTERS

The characters and character states are listed in Table 1. For the most part this is assumed to be self-explanatory, and comments on morphology and codings will be given here only where such are supposed to be needed.

Class limits for quantitative characters were set in order to minimize the number of multistate taxa.

Data on growth habit are based entirely on label data and these are with few exceptions rather superficial. It appears, however, that while the species of some genera are typically very tall trees at flowering, growing often to a height of 30 or 40 m, those of others are shrubs or small to medium-sized trees. A critical limit seems to be whether or not a species may attain a height of over 20 m. The difference between a shrubby and a treelike growth form, on the other hand, seems less taxon specific. Character 1, therefore, expresses growth
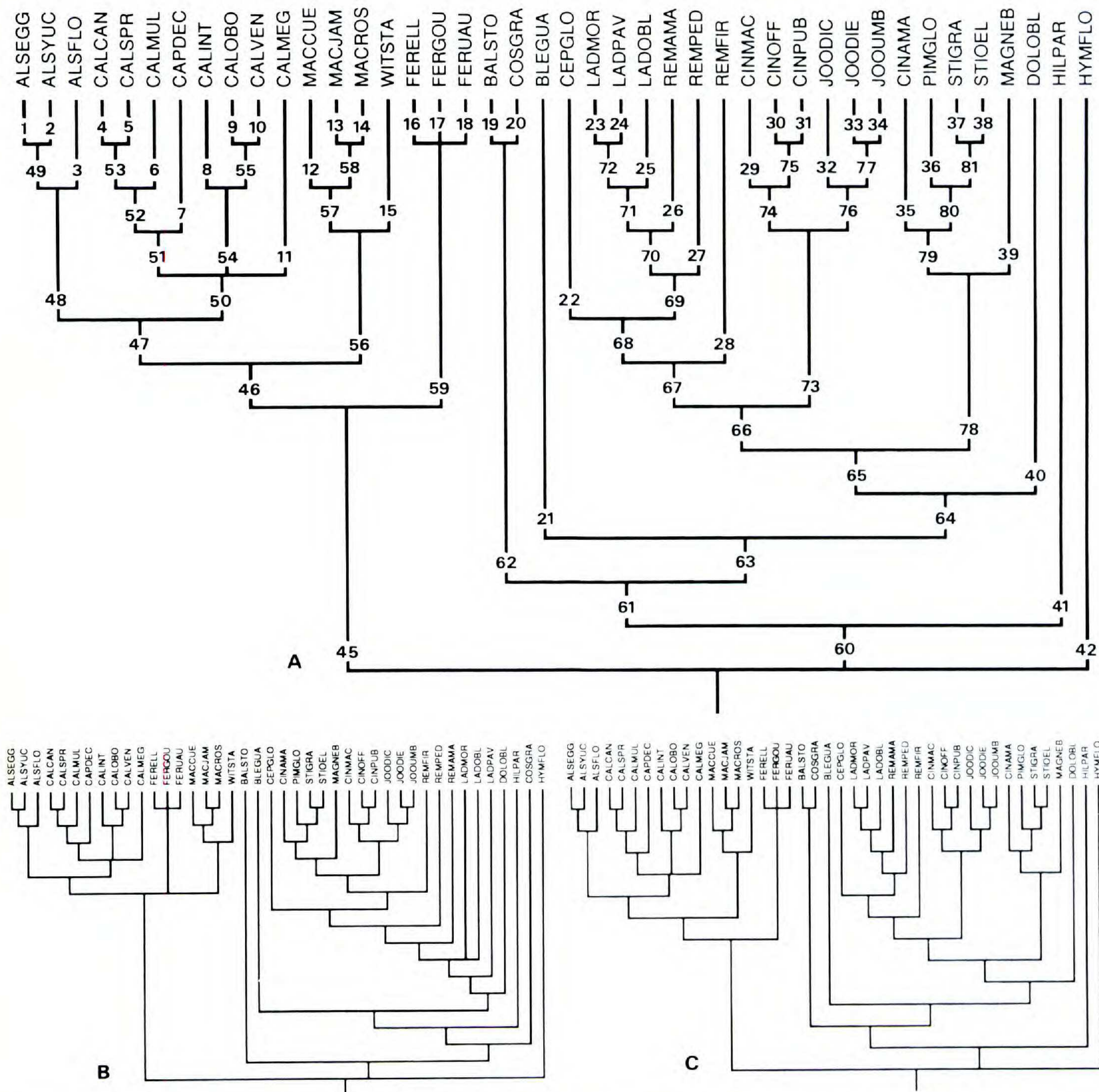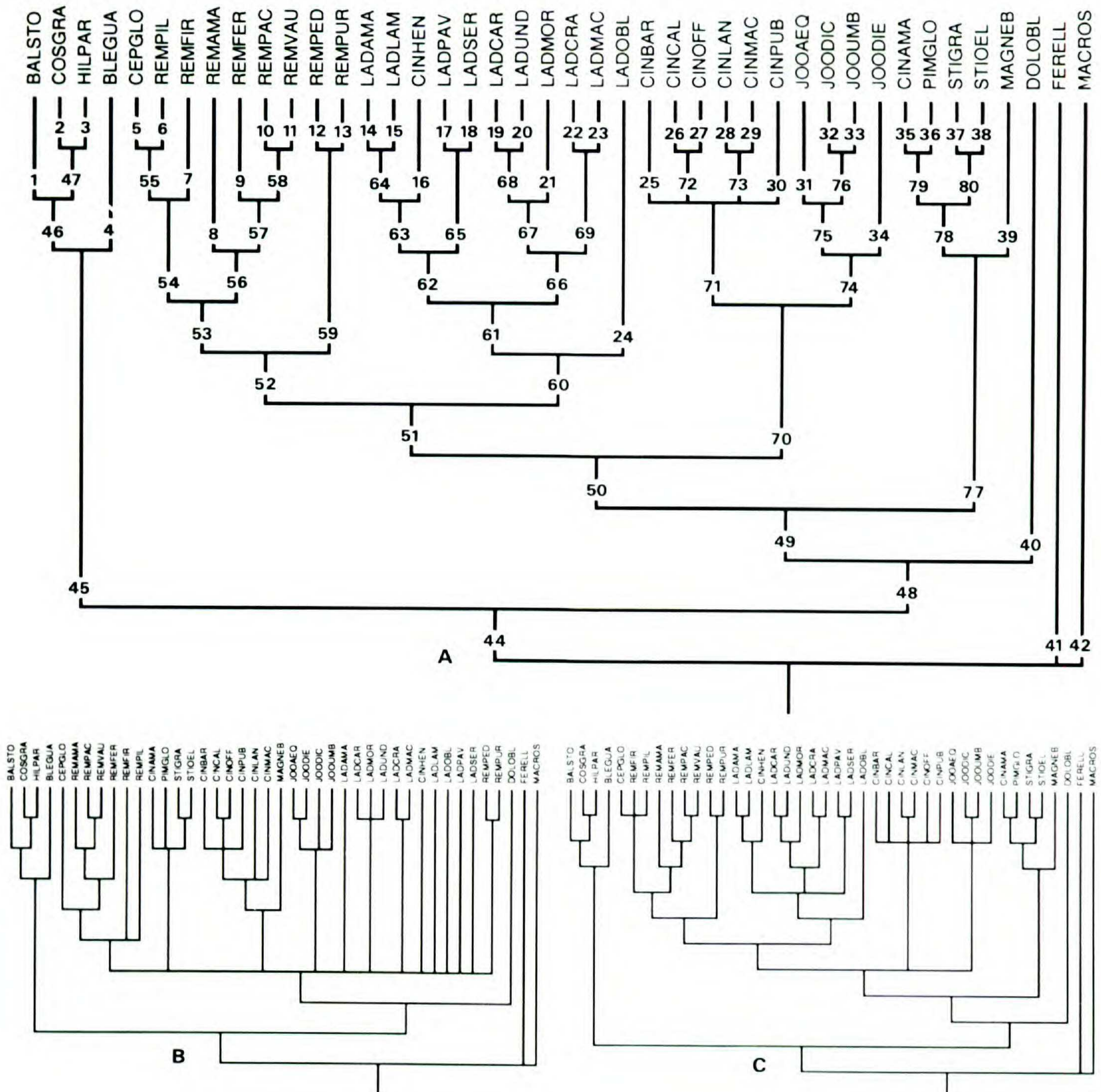
Figure 2.   Trees from the Step II analyses.—A. One out of 569 equally parsimonious minimal trees resulting after successive reweighting. Figures on edges are ordinal numbers used in the discussion and the apomorphy list.— B. Strict consensus of 1000 minimal trees saved from the search based on equally weighted characters.—C. Strict consensus of the 569 minimal trees resulting after successive reweighting. Zero length edges are collapsed. Acronyms are explained in the legend of Table 2. A complete list of apomorphies of tree A is provided in Appendix 2.

capacity rather than actual size. The figure used is the maximum height recorded for a species.

Although it may be suspected that an epiphytic or chasmophytic growth habit is typical of the tribe Hillieae (as delimited below), label data are generally too poor to make this character useful.

Stipules are regarded as caducous if shed by the formation of an abscission layer. By this definition, caducous stipules may occasionally be shed rather late and then persist for most of the life span of the leaf. On the other hand, stipules of *Joosia* are

persistent in the sense used here, although they soon die off and become much eroded. Typically, persistent stipules remain attached to the branch long after the leaf is shed.

Stipules are initiated as lateral leaf base appendages. They soon widen circumnodally, either in interpetiolar or in intrapetiolar direction, or both. Interpetiolar and intrapetiolar fusion thus seem to depend on independent growth processes and are therefore coded as independent characters.

Two different types of stipules occur with respect

Table 1.   Characters and character states.

Vegetative morphology

1—growth habit
   1 tall trees (to >20 m)
   2 smaller trees, or shrubs
2—phyllotaxy
   1 decussate
   2 whorled
3—stipule persistence
   1 caducous
   2 persistent
4—stipules: intrapetiolar fusion
   1 free
   2 partly fused
   3 fused throughout
5—stipule posture in bud
   1 held flat back-to-back
   2 clasping to contorted
   3 overlapping
6—domatia
   1 absent
   2 tuft or pouch (-with-tuft) domatia present
   3 pit or crypt domatia present
7—density of secondary leaf veins
   1 <15 pairs per 5 cm of midrib
   2 ≥15 pairs per 5 cm of midrib

Inflorescence morphology

8—terminal inflorescence
   1 present
   2 absent
9—partial inflorescences ("principal inflorescence branches")
   1 lax, dichasial or mainly so
   2 congested into headlike clusters, dichasial or mainly so
   3 ± purely monochasial
   4 thyrsoid
   5 raceme- or spike-like
   6 of solitary flowers
10—bracts and bracteoles
   1 present, plane and ± triangular
   2 present, ± sacciform
   3 absent

Floral morphology

11—flower size
   1 small, corolla tube + lobe <10 mm long
   2 medium, corolla tube + lobe 10-25 mm long
   3 large, corolla tube + lobe 25-55 mm long
   4 very large, corolla tube + lobe >55 mm long
12—heterostyly
   1 absent
   2 present
13—protogyny
   1 absent
   2 present
14—calyx shape
   1 tubular at base, with lobes 0.5-2× the length of tube

   2 tubular at base, with lobes <0.5× the length of tube (or lobes sometimes obsolete)
   3 tubular at base, with lobes >2× the length of tube
   4 ± closed in young bud, opening by a slit ("spathaceous")
   5 of free lobes
   6 reduced to minute teeth or totally obsolete
15—colleter placement inside calyx
   1 in a row at base
   2 solitary or in small groups at sinuses
   3 in groups or solitary toward base opposite sinuses
   4 scattered ± all over
   5 numerous on lobe margins at base
   - coded as missing when colleters are lacking
16—calycine semaphylls
   1 absent
   2 present at least in some flowers of an inflorescence
17—corolla aestivation
   1 valvate
   2 contorted
   3 imbricate
   4 open
   5 reduplicate
18—corolla shape
   1 campanulate
   2 salverform
   3 urceolate
   4 funnel-shaped
19—corolla color
   1 white to cream, sometimes pale greenish
   2 pink to reddish or purplish
20—corolla indumentum outside
   1 absent or sparse
   2 sericeous
   3 ± densely hirtellous
21—corolla tube indumentum inside
   1 absent
   2 hirsute above stamen attachments, with long, rigid hairs
   3 ± hirtellous or villosulous to villose above stamen attachments
   4 ± densely pubescent below stamen attachments
22—corolla tube surface inside
   1 smooth
   2 papillose above stamen attachments or throughout
   3 papillose only below stamen attachments
   4 coarsely verruculose
23—linear thinnings in corolla tissue between sinus base and filament attachment
   1 absent
   2 present
24—corolla lobe indumentum adaxially
   1 glabrous
   2 shortly papillose-hirtellous along margins

Table 1. Continued.

3 villous along margins, with long, thin-walled hairs

4 ± densely villous or hirsute all over, with thick-walled hairs

25—terminal, wedge-shaped part of corolla lobes
1 absent or inconspicuous
2 conspicuous

26—marginal, petaloid appendages of corolla lobes
1 absent
2 present

27—filament attachment
1 to basal ¼ of corolla tube
2 around middle (¼–¾ of corolla tube)
3 to distal ¼ of corolla tube

28—filament length
1 long (± equaling anther or longer)
2 short
3 long in brevistylous, short in macrostylous flowers

29—filament indumentum
1 absent
2 filaments hirsute to villous

30—anther attachment
1 dorsifixed around middle
2 dorsifixed near base
3 basifixed

31—anther presentation
1 anthers included to semi-exserted
2 anthers wholly exserted

32—anther shape
1 elongate to linear (length/width ratio ≥2)
2 button-shaped (length/width ratio <2)

33—anther base
1 obtuse
2 sagittate

34—apical connective process
1 absent
2 present

35—dorsally widened and reinforced connective
1 absent
2 present

36—disc indumentum
1 absent
2 present

37—style indumentum
1 absent
2 hirsute or puberulous distally or throughout
3 hirsute or puberulous at the very base, otherwise glabrous

38—stigma branches
1 straight, long (on the average ≥15% of style length)
2 straight, short (on the average <15% of style length)
3 strongly recurved
4 absent, stigma ± capitate

39—placenta

1 attached centrally by a lamella
2 attached apically by a stipe

Fruit morphology

40—septicidal dehiscence
1 present, basipetal
2 present, acropetal
3 absent

41—loculicidal dehiscence
1 absent
2 present, partial
3 present, ± complete

42—apical, beaklike process in mature fruit
1 absent
2 present

43—endocarp
1 thin (<0.4 mm thick)
2 thick

44—calyx presence
1 calyx present (but often much eroded) in fruit
2 calyx abscised in fruit

Seed morphology

45—hilum position
1 central or subcentral on seed body
2 marginal
3 on wing

46—seed wing shape
1 wing completely (but sometimes partly narrowly) surrounding seed body
2 wing interrupted at seed body
3 rudimentary and irregularly developed

47—seed wing margin
1 entire, irregularly lobed, or ± dented
2 deeply laciniate
3 densely ciliate/fimbriate

48—seed length (including wing)
1 small (< 4.0 mm)
2 medium (4.0–11 mm)
3 long (> 11 mm)

Vegetative anatomy

49—raphides
1 absent
2 present

50—adaxial leaf epidermis
1 1-layered
2 2- to several-layered

51—adaxial leaf cuticle
1 thin
2 thick (approaching half of epidermal cell depth, or thicker)

Pollen

52—aperture type
1 colporate with distinct colpus
2 colporate with indistinct colpus
3 porate

Table 1. Continued.

53—colpus ends
    1 acute
    2 obtuse to truncate
54—os
    1 clearly demarcated with regular, often slightly thickened margin
    2 poorly demarcated with irregular margin
55—tectum perforation type
    1 reticulate (lumen/muri ratio >1.0)
    2 foveolate (lumen/muri ratio <1.0)
    3 imperforate
56—lumen differentiation into two distinct size classes
    1 absent
    2 present
57—latitudinal differentiation of lumina
    1 absent, or lumina smaller toward colpi
    2 lumina larger toward colpi

58—columella length
    1 long (≥ 0.5 μm)
    2 medium (0.15–0.4 μm)
    3 short (< 0.15 μm)

Seed anatomy
  59—wall thickenings of inner tangential wall
    1 meshwork or broad bands
    2 plate with large pores
    3 walls not thickened, or thickening an undifferentiated sheet
  60—spinules or verruculae on secondary wall inside
    1 absent
    2 present

to their posture in bud. They are either held flat back-to-back, and are then usually lingulate to obovate and herbaceous in texture, or they are clasping to contorted, forming a cone over vegetative buds, and then more or less triangular and usually brownish and more or less coriaceous in texture. When the stipules are fused throughout both inter- and intrapetiolarly to form a calyptra, this character does not apply and was coded as missing data.

In *Joosia* the branching of partial inflorescences is predominantly monochasial, more or less boragoid shoot chains arising as lateral branches from a basal dichasial branching. In *Joosia aequatoria* and *J. dielsiana*, with more or less congested inflorescences, the boragoid branches are often short and few-flowered. In these cases it is dubious whether inflorescence branching should be coded as dichasial or monochasial, occasional monochasial branchings being common in cymes of the Rubiaceae. Based on observations of a number of collections of *J. dielsiana* with longer inflorescence branches it was concluded that this ambiguous situation has arisen through reduction of longer monochasial branch systems. The inflorescence branches of *J. aequatoria* and *J. dielsiana* are therefore coded as monochasial.

In *Remijia* inflorescences are typically thyrsoid. In several species, like *R. pilosinervula*, where the thyrses are few-tiered, reduction series occur, from several-tiered to 1-tiered thyrses. In the extreme such inflorescences may appear to be highly condensed dichasia. In such cases these inflorescences were coded as thyrsiform, however.

When the available flowering collections are few it may be impossible to decide whether the species is heterostylous. Macrostylous flowers in heterostylous species are not strikingly different from flowers of monomorphic species, and in some of the heterostylous species examined the number of macrostylous plants may exceed that of brevistylous ones by one to ten. The following coding practice was followed. In genera where heterostyly was documented to be common (*Cinchona, Joosia, Ladenbergia,* and *Remijia*), the species were coded as heterostylous if the brevistylous morph was encountered, otherwise as missing data. In other genera, where heterostyly has never been documented, species were coded as homostylous on the basis of single observations of long-styled flowers.

In *Dolicholobium* the flowers are functionally unisexual (on monoecious plants), with the nonfunctional organs vestigial. Because this character state is autapomorphic in the present data set, it was not included in the analysis and *D. oblongifolium* was coded as homostylous, the difference in style development between flower morphs being obviously non-homologous with heterostyly in other genera.

The presence of colleters on the inside of the calyx is highly unpredictable, even within species. When present, however, the number and placement of colleters is fairly constant within species. Therefore, states were assigned to placement and grouping of colleters, while absence of colleters was coded as missing data.

Corolla aestivation in some species of *Cosmibuena* was described as quinquncial by Taylor

Table 2. Complete data matrix. Acronyms: ALSEGG = *Alseis eggersii* Standley, ALSFLO = *A. floribunda* Schott in Sprengel, ALSYUC = *A. yucatanensis* Standley, BALSTO = *Balmea stormae* Martínez, BLEGUA = *Blepharidium guatemalense* Standley, CALCAN = *Calycophyllum candidissimum* (M. Vahl) DC., CALINT = *C. intonsum* Steyerm., CALMEG = *Calycophyllum megistocaulum* (Krause) C. M. Taylor, CALMUL = *C. multiflorum* Griseb., CALOBO = *C. obovatum* (Ducke) Ducke, CALSPR = *C. spruceanum* (Benth.) J. D. Hook., CALVEN = *C. venezuelense* Steyerm., CAPDEC = *Capirona decorticans* Spruce, CEPGLO = *Cephalodendron globosum* Steyerm., CINAMA = *Cinchona amazonica* Standley, CINBAR = *C. barbacoensis* Karsten, CINCAL = *C. calisaya* Wedd., CINLAN = *C. lancifolia* Mutis, CINHEN = *C. henleana* Karsten, CINMAC = *C. macrocalyx* Pavón ex DC., CINOFF = *C. officinalis* L., CINPUB = *C. pubescens* M. Vahl, COSGRA = *Cosmibuena grandiflora* (Ruiz López & Pavón) Rusby, DOLOBL = *Dolicholobium oblongifolium* A. Gray, FERELL = *Ferdinandusa elliptica* Pohl, FERGOU = *F. goudotiana* Schumann, FERUAU = *F. uaupensis* Spruce ex Schumann, HILPAR = *Hillia parasitica* Jacq, HYMFLO = *Hymenodictyon floribundum* (Hochst. & Steud.) Robinson, JOOAEQ = *Joosia aequatoria* Steyerm., JOODIC = *J. dichotoma* (Ruiz López & Pavón) Karsten, JOODIE = *J. dielsiana* Standley, JOOUMB = *J. umbellifera* Karst., LADAMA = *Ladenbergia amazonensis* Ducke, LADCAR = *L. carua* (Wedd.) Standley, LADCRA = *L. crassifolia* (DC.) Standley, LALDLAM = *L. lambertiana* (C. Martius) Klotzsch in Hayne, LADMAC = *L. macrocarpa* (M. Vahl) Klotzsch in Hayne, LADMOR = *L. moritziana* Klotzsch in Hayne, LADOBL = *L. oblongifolia* (Mutis) L. Andersson, LADPAV = *L. pavonii* (Lambert) Standley, LADSER = *L. sericophylla* Standley, LADUND = *L. undata* Klotzsch in Hayne, LUCINT = *Luculia intermedia* Hutch., MACCUE = *Macrocnemum cuencanum* Standley, MACJAM = *M. jamaicense* L., MACROS = *M. roseum* (Ruiz López & Pavón) Wedd., MAGNEB = *Maguireocharis neblinae* Steyerm., PIMGLO = *Pimentelia glomerata* Wedd., REMAMA = *Remijia amazonica* Schumann, REMFER = *R. ferruginea* (A. St. Hil.) DC., REMFIR = *R. firmula* (C. Martius) Wedd., REMPAC = *R. pacimonica* Standley, REMPED = *R. pedunculata* (Karsten) Flückiger, REMPIL = *R. pilosinervula* Steyerm., REMPUR = *R. purdieana* Wedd., REMVAU = *R. vaupesiana* Steyerm., STIGRA = *Stilpnophyllum grandifolium* L. Andersson, STIOEL = *S. oellgaardii* L. Andersson, WITSTA = *Wittmackanthus stanleyanus* (R. M. Schomb.) Kuntze.

Row labels (top to bottom): ALSEGG, ALSFLO, ALSYUC, BALSTO, BLEGUA, CALCAN, CALINT, CALMEG, CALMUL, CALOBO, CALSPR, CALVEN, CAPDEC, CEPGLO, CINAMA, CINBAR, CINCAL, CINLAN, CINHEN, CINMAC, CINOFF, CINPUB, COSGRA, DOLOBL, FERELL, FERGOU, FERUAU, HILPAR, HYMFLO, JOOAEQ, JOODIC

Column headers: 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60

Table 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
JOODIE	2	2	2	1	1	1	1	1	3	3	23	2	1	12	2	1	1	2	2	2	1	1	1	1	1	2	2	2	2	2	1	1	1	2	1	2	1	1	1	1	2	1	1	1	1	1	1	2	1	2	1	1	2	2	2	1	1	2	3	1
JOOUMB	2	2	2	1	1	1	1	1	3	3	2	2	1	12	2	1	1	2	1	2	1	1	1	2	2	2	2	2	2	2	1	1	1	1	1	2	1	1	1	1	3	1	1	1	1	1	2	2	1	1	2	1	2	2	2	1	2	2	1	1
LADAMA	1	1	1	1	1	2	1	1	1	1	23	2	1	1	2	1	2	2	1	2	1	2	1	2	2	1	23	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	2	1	1	2	2	2	1	2	3	1	1
LADCAR	2	1	1	1	1	12	1	1	1	1	3	2	1	12	3	1	1	2	1	2	1	2	2	2	2	1	2	2	1	2	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	2	12	3	1	2	2	1	2	2	2	2	1	2	2	1
LADCRA	2	1	1	3	2	1	1	1	1	1	3	2	1	12	1	1	1	2	1	2	1	1	2	2	2	1	2	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	23	1	2	1	1	2	2	2	2	2	3	2	1
LADLAM	2	1	1	12	1	2	1	1	1	1	23	2	1	2	2	1	1	2	1	2	1	4	1	2	2	1	23	2	1	2	1	1	1	1	1	12	1	1	1	1	1	1	2	1	1	1	23	1	1	12	1	1	2	2	23	1	2	2	1	1
LADMAC	2	1	1	3	1	12	1	1	1	1	34	2	1	1	1	1	1	2	1	2	1	4	1	2	2	1	2	2	1	2	2	1	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	3	1	2	1	1	2	2	2	2	2	2	1	1
LADMOR	2	1	1	2	2	1	1	1	1	1	34	2	1	3	2	1	1	2	1	2	1	2	2	2	2	1	2	2	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	1	1	2	2	23	1	2	1	1	2	2	2	2	2	2	1	1
LADOBL	1	1	1	2	1	2	1	1	1	1	2	2	1	123	2	1	1	2	1	2	1	1	1	2	2	1	12	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	3	1	2	1	1	2	2	2	2	2	2	1	1
LADPAV	2	1	1	2	2	2	1	1	1	1	4	1	1	2	3	1	1	2	1	2	1	2	2	2	2	1	2	2	1	2	1	2	1	1	1	1	1	2	1	1	3	1	2	1	3	2	1	3	1	2	2	1	2	2	2	1	2	2	1	1
LADSER	2	1	1	2	1	1	1	1	1	1	4	2	1	1	3	1	1	2	1	2	1	1	3	1	2	1	2	2	1	2	1	2	1	1	1	1	2	2	3	3	3	1	1	1	3	2	2	3	1	2	2	1	2	1	2	1	2	2	1	1
LADUND	2	1	1	2	1	1	1	2	1	1	23	1	1	5	2	1	1	2	1	2	2	3	2	2	2	1	2	2	2	2	2	2	1	1	1	1	2	2	3	3	3	1	1	1	3	2	1	3	1	1	2	1	1	1	1	2	1	2	1	1
LUCINT	2	1	1	1	2	2	1	2	1	1	3	1	1	12	3	1	5	2	2	1	12	3	2	4	2	1	2	1	1	1	2	2	1	2	1	1	1	1	2	2	1	1	2	2	3	2	1	1	1	1	2	2	1	2	12	2	2	2	2	1
MACCUE	2	1	1	2	1	1	1	2	1	1	2	1	1	12	5	1	5	2	1	1	3	3	2	2	2	1	2	1	2	1	2	2	1	2	1	1	1	2	3	3	3	1	2	1	3	2	2	1	2	1	2	2	1	2	1	2	2	2	1	1
MACJAM	2	1	1	2	1	2	1	2	1	1	2	1	1	123	3	1	5	2	1	1	12	3	1	2	2	1	2	1	2	1	2	2	1	1	1	1	1	2	2	3	3	1	2	1	3	1	3	2	1	1	2	2	1	2	1	2	2	2	2	1
MACROS	1	1	1	1	1	12	1	2	1	1	2	1	1	3	2	1	5	2	1	1	3	2	1	2	2	1	2	1	1	1	2	2	1	1	1	1	1	1	2	1	2	1	1	1	1	1	3	1	12	1	1	1	1	1	12	12	1	1	1	1
MAGNEB	2	1	1	2	1	1	1	1	1	1	2	1	1	1	2	1	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	2	1	1	1	1	12	12	1	1	1	1	12	1	1	1	1	1	12	1	2	1	1	2	2	1	1	2	1	1
PIMGLO	2	2	1	1	2	2	1	2	1	1	1	1	1	1	2	1	1	2	2	2	4	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1	2	2	1	1	2	1	2	1	2	1	1	2	2	1	2	2	1	2	2	1	1
REMAMA	2	2	1	12	3	1	1	2	4	1	2	2	1	12	3	1	1	2	1	2	1	1	1	2	2	1	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	2	2	2	2	2	1	1	2	1	1
REMFER	2	2	1	3	1	12	1	2	4	1	23	2	1	1	3	1	1	2	1	1	2	2	2	2	2	1	2	2	2	2	2	2	1	1	1	1	3	2	2	1	1	1	1	1	1	1	3	2	1	1	2	2	2	2	2	2	2	2	1	1
REMFIR	2	2	1	1	1	1	1	2	4	1	2	2	1	2	2	1	1	2	2	1	3	1	1	2	2	1	2	1	1	2	1	1	1	1	1	1	3	1	1	1	1	1	1	2	1	2	1	2	1	2	2	1	2	2	2	1	2	2	1	1
REMPAC	2	2	1	1	3	2	1	2	4	1	2	2	1	12	3	1	1	2	1	2	3	1	1	2	2	1	2	2	1	2	1	1	1	1	1	1	3	2	1	1	2	1	1	1	1	1	3	3	1	1	2	2	2	2	2	2	2	2	1	2
REMPED	2	2	1	2	1	12	1	2	4	1	12	2	1	12	3	1	1	2	2	2	1	1	1	2	2	1	2	2	1	2	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	3	12	12	1	2	2	2	2	2	1	1	1	1	1
REMPIL	2	1	1	1	1	2	1	2	4	1	12	2	1	12	2	1	1	2	12	1	12	1	1	2	2	1	2	2	1	2	1	1	1	1	12	12	1	1	1	1	2	1	1	1	1	1	3	12	1	1	2	2	2	2	12	1	2	2	1	1
REMPUR	2	2	1	2	1	2	2	2	4	1	2	2	1	3	2	1	1	2	1	2	3	1	1	2	2	1	2	2	1	2	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	2	1	1	1	1	2	2	2	2	12	1	2	2	1	1
REMVAU	2	2	1	1	1	2	1	2	4	1	2	2	1	2	2	1	1	2	1	2	1	1	1	2	2	1	2	2	1	2	1	1	1	1	1	1	3	2	1	1	2	1	1	1	1	1	3	3	1	1	1	1	2	2	1	1	2	3	2	1
STIGRA	2	1	1	2	3	2	2	2	4	1	3	3	1	2	3	1	1	2	2	2	3	1	1	2	2	1	2	2	1	2	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	3	1	2	1	1	2	2	2	2	2	3	1	1
STIOEL	2	1	1	2	1	2	2	2	1	1	2	2	1	2	2	1	1	2	2	2	3	1	1	2	2	1	2	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	2	2	1	2	2	1	1
WITSTA	1	1	1	2	2	2	1	1	5	1	12	1	1	3	2	2	3	2	3	3	2	2	1	1	1	3	3	1	1	1	2	1	1	1	1	1	3	4	1	1	2	1	1	2	1	2	1	1	1	2	1	1	2	2	2	1	2	2	1	1

(1994). However, according to accepted usage (e.g., Stearn, 1983) quinquncial is a special case of imbricate. In *Hillia, Cosmibuena,* and *Dolicholobium* the petals occur in two layers (typically three in the outer and two in the inner layer), being typically contorted in each layer. Aestivation is therefore coded as contorted in these taxa.

In *Cinchona* filament length differs considerably between brevistylous and macrostylous flower morphs. This is coded as a separate character state under character 28. In cases where only macrostylous flowers were seen this character is coded as missing data.

Stigma branch length (character 38) in heterostylous species was calculated on the basis of the macrostylous morph. In cases where only the brevistylous morph was observed, style length of the macrostylous morph was approximated to equal corolla tube length and the value was accepted if well separated from the class limit; if close to the class limit, the character was coded as missing data.

Pollen characters were discussed and documented in detail by Andersson (1993).

RESULTS AND DISCUSSION

Throughout this discussion, clades will be designated by the numbers (Figs. 1 and 2) of the edges supporting them. Terminal taxa will be referred to by their traditional names, on which the acronyms used in the trees are based; a number of new names and combinations are introduced in the Synopsis. Only selected characters will be discussed here; complete apomorphy lists for the trees of Figures 1A and 2A are given in Appendix 2.

The Step I analysis run with unweighted characters resulted in 24 equally parsimonious trees with a length of 286 steps and an overall consistency index of 0.490. Successive reweighting gave nine equally parsimonious trees 289 steps long (calculated on the basis of unweighted characters) and with a consistency index of 0.484. Using Archie's (1989: 267) empirical formula, homoplasy excess ratio (HER) for the tree of Figure 1A was estimated at 0.587.

Both with weighted and unweighted characters, a basal dichotomy was found between clades 45 and 60 (Fig. 1A). Clade 45 is not supported by any unique and consistent apomorphies, but by three rare character states, long filaments (with parallelisms in *Pimentelia* and *Stilpnophyllum*), anthers fully exserted (with reversal in *Capirona*), and anthers button-shaped (with reversals in *Capirona* and *Wittmackanthus*). Clade 45 contains all genera (except *Schizocalyx*) referred to the

Calycophylleae by Andersson & Persson (1991), plus three genera referred by them to the Cinchoneae: *Capirona, Ferdinandusa,* and *Macrocnemum. Macrocnemum* and *Capirona* are further nested in clade 45 by the presence of bristly hairs in the corolla tube and on the filaments, and by the interruption of the seed wing at the seed body. All are excluded from clade 60 by the lack of the apomorphic pollen characters foveolate exine and obtuse colpus ends. The conclusion seems well founded, therefore, that *Capirona, Ferdinandusa,* and *Macrocnemum* should be transferred to the Calycophylleae.

Calycophyllum in the traditional sense of, for example, Bacigalupo (1952) and Steyermark (1964, 1974) is divided between two clades, one (52) comprising the type species, *C. candidissimum,* and two closely related species, the other one (54) comprising the so-called "*Calycophyllum obovatum* group" (Steyermark, 1964). *Calycophyllum megistocaulum* (= *C. acreanum* Ducke), considered by Steyermark (1964) to be closely related to the "*C. obovatum*" group, is nested in clade 50 by virtue of its huge size, and small flowers with a campanulate corolla, but its position within the clade is not resolved. *Capirona* is nested in clade 50 on the basis of, among other things, huge size and presence of calycine semaphylls. It is nested in clade 51 also on the basis of the verruculose inside of its exotesta cells. *Capirona* is well characterized by several unique autapomorphies such as intrapetiolar stipules (stipules fused throughout intrapetiolarly and deeply divided interpetiolarly) and its unique exine structure (Andersson, 1993). This, taken together with the fact that clade 52 is likewise supported by several unique synapomorphies, makes it rather unattractive to merge *Capirona* with *Calycophyllum.* In consequence, *Calycophyllum* will have to be split into two genera, *Calycophyllum* s. str. (clade 52) and *Semaphyllanthe* (clade 54), described as a new genus in the Synopsis.

Calycophyllum s. str. (clade 52) is supported as monophyletic by three unique synapomorphies, i.e., sacciform bracts and bracteoles, calyx reduced to minute teeth, and filaments inserted at the sinuses. It is further supported by having corolla lobes imbricate in bud (parallelisms in *Wittmackanthus* and *Blepharidium*). *Semaphyllanthe* (clade 54) is supported only by more or less strongly homoplasious characters.

Alseis (clade 48) is well supported as monophyletic by five unique synapomorphies: protogynous flowers, corolla open in bud (reversed in at least one species excluded from this analysis), corolla

urceolate, puberulous style (reversed in several species excluded from this analysis), and placenta attached apically by a stipe. It is further supported by two rare character states that are more or less constant in the genus: subspicate (reduced thyrsiform) inflorescences (parallelisms in *Wittmackanthus* and *Hymenodictyon*), and filaments attached close to the corolla base (parallelism in *Calycophyllum intonsum*). Its sister-group relationship (clade 47) to the *Calycophyllum* group is supported by long recurved stigma branches (numerous reversals in the *Calycophyllum* group) and verruculose thickenings on the inner tangential wall of exotesta cells (reversal in *Calycophyllum intonsum*).

Ferdinandusa (clade 59) is supported as monophyletic by three unique synapomorphies: colleters placed in a continuous row along the base on the inside of the calyx, connective dorsally widened and reinforced, and lumina of the exine differentiated into two distinct size classes. It is further supported by one rare character state, large seed size (parallelisms in species of *Ladenbergia* and *Remijia*).

Macrocnemum (clade 57) is supported as monophyletic by three unique synapomorphies: corolla reduplicate in bud, corolla tube minutely papillose inside below the stamen attachments, and fruits loculicidally dehiscent throughout. It is further supported by three rare apomorphic character states: corolla lobes marginally minutely papillose (parallelisms in *Ladenbergia* and *Remijia*), thinnings in the corolla tube tissue running down from the sinuses to the stamen attachments (parallelism in *Cinchona*), and inner tangential wall of the exotesta cells with sheetlike secondary thickening with pores (parallelism in *Joosia dichotoma*).

The sister-group relationship between *Macrocnemum* and *Wittmackanthus* (clade 56) is supported only by homoplasious characters (reddish corolla, small seeds, foveolate exine). Steyermark & Kirkbride (1975) concluded that the closest relative of *Wittmackanthus* is *Calycophyllum*. However, *Wittmackanthus* lacks the critical synapomorphies of the *Calycophyllum* group, such as internally verruculose exotesta cells and curved style branches. Its position within the Calycophylleae seems rather uncertain.

Clade 60, which includes the remaining genera of the Cinchoneae and *Hillia*, is supported as monophyletic by a single unique synapomorphy in the runs of Step I, obtuse to truncate colpus ends (further transformed in *Blepharidium* and *Dolicholobium*, where pollen grains are porate).

Step II (Fig. 2) generated more than 1000 min-

imal trees in the run with unweighted characters, 234 steps long and with overall consistency indices of 0.490. After successive reweighting 569 minimal trees were found, 235 steps long (as calculated with unweighted characters) and with overall consistency indices of 0.579. The HER for the tree of Figure 2A was estimated at 0.485.

The differences in topology between the trees from Step I (Fig. 1) and those from Step II (Fig. 2) are striking. These differences seem to depend mainly on the fact that different outgroups are used. Since a closer outgroup is used in Step II, and since the ingroup contains a fuller selection of terminal taxa, edge lengths are shorter on the average. One is therefore justified in putting greater confidence in the results of Step II than those of Step I (see, e.g., Penny et al., 1992).

The ingroup (clade 44) is supported as monophyletic by four unique synapomorphies: included anthers, elongate to linear anthers, long connivent stigma branches, and obtuse to truncate colpus ends. It is further supported by two homoplastic character states: short filaments (reversed in *Pimentelia* and *Stilpnophyllum*) and foveolate tectum (reversed in *Hillia parasitica* and with further parallel transformations to psilate in *Blepharidium*, internally in *Cosmibuena grandiflora*, and in *Dolicholobium*).

Dolicholobium comes out as a basal clade (40) in Step II analyses, in contrast to those of Step I, where it comes out in a more distal position within a basal paraphyletic complex. Its position was variable also among the preliminary runs. This uncertainty may indicate that the assumption that it belongs to the Cinchoneae complex is faulty.

Both the run with unweighted and that with weighted characters indicate a basal dichotomy between one clade (45) comprising *Balmea*, *Blepharidium*, *Cosmibuena*, and *Hillia*, and another one (48) comprising *Cephalodendron*, *Cinchona*, *Dolicholobium*, *Joosia*, *Ladenbergia*, *Maguireocharis*, *Pimentelia*, *Remijia*, and *Stilpnophyllum*. This result is interpreted as support for the recognition of an extended tribe Hillieae (clade 45) that is the sister group of the tribe Cinchoneae (clade 48).

The tribe Hillieae (clade 45) is supported by one unique and consistent synapomorphy, fruit with an apical, beaklike prolongation, and also by the rare character state calyx shed in fruit (parallelisms in *Cephalodendron* and *Wittmackanthus*). The "central core" of the tribe (clade 46) is furthermore supported by presence of raphides. The phylogeny of this tribe (excluding *Blepharidium*) was studied in detail by Taylor (1994).

The tribe Cinchoneae (clade 48) is supported as monophyletic by an externally sericeous corolla (reversals in *Stilpnophyllum grandifolium* and *Maguireocharis*). If *Dolicholobium* is excluded (clade 49) it is supported by another two unique and consistent synapomorphies, corolla lobes valvate in bud and os of the pollen aperture poorly defined.

The genera *Maguireocharis, Pimentelia,* and *Stilpnophyllum*, together with *Cinchona amazonica*, form a monophyletic group (clade 77) that is the sister group of the rest (clade 50) of the Cinchoneae. Clade 77 is supported as monophyletic by two synapomorphies, corolla tube hirsute inside above stamens and corolla lobes hirsute all over adaxially. It is also set aside from the rest of the Cinchoneae by lacking the unique and consistent synapomorphy of clade 50, heterostylous flowers. The genus *Stilpnophyllum* (clade 80) is supported as monophyletic by its unusual leaf venation, with secondary veins very thin and closely set. Clade 79 is supported as monophyletic by a campanulate corolla, but since this character may easily be erroneously interpreted in very short-tubed flowers, it should not be overemphasized. Clade 78 is supported only by homoplastic characters. *Cinchona amazonica* must obviously be removed from the genus *Cinchona* (clade 71), in which it was supposedly originally placed based mainly on its acropetal fruit dehiscence. Recognizing that the resolution of clade 77 may not be particularly stable, I suggest that it be referred to a genus of its own, *Cinchonopsis*, formally described in the Synopsis.

The sister group relationship of *Cinchona* and *Joosia* (clade 70) is supported by the joint possession of reddish flowers, a character with several parallelisms and also reversals within *Joosia*. It is not supported in all solutions (Fig. 2C), and the two genera may come out as successive basal branchings of clade 50. Both genera are excluded from clade 51 by lack of two unique synapomorphies.

Joosia (clade 74) is supported as monophyletic by four unique and consistent synapomorphies: persistent stipules, predominantly monochasial partial inflorescences, corolla lobes with submarginal, showy appendages, and inner tangential exotesta walls with sheetlike thickening. It is further supported by absence of inflorescence bracts (parallelism in *Dolicholobium*) and hairy disk (parallelisms in *Cinchona calisaya* and *C. amazonica*). The segregation of *Joosia dichotoma* as a distinct subgenus, *Sectocalyx*, as suggested by Steyermark (1975), would leave the autonymous subgenus *Joosia* paraphyletic. Steyermark seems to have based his de-

cision entirely on the occurrence in *J. dichotoma* of a unique autapomorphy, the spathaceous calyx.

Cinchona (clade 71) is supported as monophyletic by two unique and consistent synapomorphies, corolla lobe margins villous with thin-walled hairs and filaments distinctly different in length in brevi- and macrostylous flowers. It is further supported by the corolla tube with longitudinal thinnings (parallelism in *Macrocnemum*) and acropetal fruit dehiscence (consistent but with numerous parallelisms in *Ladenbergia* and *Remijia*). *Cinchona henleana*, traditionally (e.g., Standley, 1930, 1931a; Steyermark, 1974) included in *Cinchona* on the basis of its acropetally dehiscent fruits, is nested within the *Ladenbergia* clade and should be removed (see further below).

The sister-group relationship (clade 51) between *Ladenbergia* and *Remijia* is supported by two unique and consistent synapomorphies, corolla lobes with the apical part ridged and wedge-shaped and corolla lobe margins papillose. These two character states are conceivably functionally coupled, which may weaken the support for the clade.

Ladenbergia (clade 60) is supported as monophyletic by only two homoplasious characters, stipules fused at base (with several reversals and parallelisms, and a further transformation to fused throughout in clade 69) and large seeds (parallelism in clade 58). *Cinchona henleana* is nested within the *Ladenbergia* clade. It seems, intuitively, closely related to, if at all distinct from, two other species traditionally (e.g., Standley, 1930) treated here, *L. muzonensis* (Goudot) Standley and *L. hookeriana* (Wedd.) Standley. These two were separated as section *Muzonia* by Weddell (1849) and later elevated to generic rank by Osorio (1874). Judging from the present analysis, the recognition of *Muzonia*, as advocated by Sullivan & Steyermark (1983) would, however, force a fragmentation of the remaining part of *Ladenbergia* and seems, therefore, to be ill advised. The sections recognized by Weddell (1849) under the synonymous name *Cascarilla* seem to be in fair agreement with the present results, but are not really put to the test due to only partial correspondence in selection of taxa.

The genus *Remijia* (clade 52) is supported as monophyletic by one synapomorphy, terminal inflorescence absent, which is consistent but with numerous parallelisms. Clade 53, comprising all species except *R. pedunculata* and *R. purdieana* (clade 59), is further characterized by a unique synapomorphy, thyrsoid inflorescences (further transformed to capitate in *Cephalodendron globosum*). Clade 59 is supported as monophyletic by

marginally ciliate seed wings. The apically split capsule valves (fruit with partial loculicidal dehiscence), traditionally emphasized as a distinctive character of *Remijia*, is a highly homoplasious one. The genus *Cephalodendron* is nested within the *Remijia* clade and should be regarded as an apomorphic derivative of this genus; recognition of *Cephalodendron* would force the pulverization of *Remijia*.

SYNOPSIS

Tribe **Calycophylleae** L. Andersson & C. Persson, Pl. Syst. Evol. 178: 89. 1991. TYPE: *Calycophyllum* DC.

Trees or rarely shrubs. Raphides absent. Stipules usually clasping to contorted in bud, rarely held flat back-to-back, or calyptrate. Corolla lobes contorted, imbricate, open, or reduplicate in bud; filaments long, often bristly hirsute at base, anthers button-shaped to elongate, rarely linear, dorsifixed near middle, or basifixed; ovary multiovulate, with distinct placentae attached to septum by a lamella, or apically by a stipe. Pollen 3-colporate, the colpi with acute ends and os distinctly demarcated, or rarely 3-porate, exine usually reticulate, rarely ± foveolate. Fruit a usually septicidal capsule with a short loculicidal fissure at apex of valves, or (*Macrocnemum*) loculicidal. Seeds lenticular or planoconvex, with exotestal wing, hilum located centrally or marginally on seed body, or on wing, exotesta cells with bandlike thickenings on inner tangential wall, or (in *Macrocnemum*) the thickening sheetlike with pores.

Alseis Schott in Sprengel, Syst. Veg. 4(2): 404. 1827. TYPE: *Alseis floribunda* Schott in Sprengel.

Alseis is recognized by its subspicate (reduced thyrsiform) inflorescences, protogynous flowers with urceolate corolla having the lobes usually open in bud, and its pendent placentae. It is a neotropical genus supposed (Andersson, 1992) to comprise about 16 species. It is badly in need of taxonomic revision, however.

Calycophyllum DC., Prodr. 4: 367. 1830. TYPE: *Macrocnemum candidissimum* M. Vahl = *Calycophyllum candidissimum* (M. Vahl) DC.

Eukylista Benth., J. Bot. (Hooker) 5: 230. 1853. TYPE: *Eukylista spruceana* Benth. = *Calycophyllum spruceanum* (Benth.) J. D. Hook. ex Schumann.

Calycophyllum is recognized by its calyptrate stipules and sacciform bracts and bracteoles, calyx

(except semaphylls) reduced to minute teeth (to sometimes totally obsolete), corolla lobes that are imbricate in bud, filaments inserted on the corolla at the sinuses, corolla tube bristly hirsute inside in the upper part, and glabrous filaments. It is a genus of three species distributed from northern Central America and the Greater Antilles to northern Argentina and Paraguay.

Capirona Spruce, J. Proc. Linn. Soc., Bot. 3: 200. 1859. TYPE: *Capirona decorticans* Spruce.

Monadelphanthus Karsten, Fl. Columb. 1: 67. 1860. TYPE: *Monadelphanthus floridus* Karsten = *Capirona decorticans* Spruce.
Loretoa Standley, Field Mus. Nat. Hist., Bot. Ser., 11: 221. 1936. TYPE: *Loretoa peruviana* Standley = *Capirona decorticans* Spruce.

Capirona is recognized by its intrapetiolar, persistent stipules, corolla with lobes contorted in bud and tube conspicuously plicate, filaments inserted near the base of the corolla tube and interconnected at base by a callosity, basifixed anthers, pollen with reticulate exine with very narrow muri, wide lumina, and numerous free, rodlike structures within the lumina, and by seeds with the hilum located on the wing. It is a monotypic genus (Andersson, 1994) distributed more or less throughout the Amazon basin and the Guianas.

Semaphyllanthe L. Andersson, gen. nov. TYPE: *Semaphyllanthe obovata* (Ducke) L. Andersson = *Calycophyllum obovatum* (Ducke) Ducke = *Warszewiczia obovata* Ducke.

Calycophyllo similis sed differt stipulis liberis, bracteis planis, calyce distincto, corolla aestivatione contorta, filamentis ad basin hirsutis, ad medium corollae tubo, vel basin versus affixis.

Trees. Leaves decussate; stipules interpetiolar, not fused at base, ± triangular, clasping in bud, caducous. Inflorescences terminal and lateral, cymose, clustered to form ± corymbose synflorescences at branch tips. Flowers small, homostylous, normally 4-merous; calyx ± cup-shaped, with distinct or indistinct lobes, some flowers usually (except in *S. megistocaula*) with one of the lobes expanded into a large semaphyll; corolla ± campanulate, tube ± equaling the lobes, or shorter, glabrous outside, densely bristly hirsute inside above stamen insertion, lobes contorted in bud, glabrous; stamens attached to corolla tube in central part or lower, filaments longer than anthers, bristly hirsute in lower part; anthers button-shaped, dorsifixed near middle, long exserted; stigma branches con-

nivent or widely recurved. Capsules septicidal with basipetal dehiscence, crowned by the persistent calyx. Seeds winged, hilum located ± centrally on seed body, exotesta cells with bandlike, ± verruculose secondary thickenings on inner tangential wall.

SPECIES INCLUDED:

Semaphyllanthe intonsa (Steyerm.) L. Andersson, comb. nov. Basionym: *Calycophyllum intonsum* Steyerm., Mem. New York Bot. Gard. 10(5): 186. 1963.

Semaphyllanthe megistocaula (K. Krause) L. Andersson, comb. nov. Basionym: *Remijia megistocaula* K. Krause, Bot. Jahrb. 40: 319. 1908.

Semaphyllanthe merumensis (Steyerm.) L. Andersson, comb. nov. Basionym: *Calycophyllum merumense* Steyerm., Mem. New York Bot. Gard. 23: 228. 1972.

Semaphyllanthe obovata (Ducke) L. Andersson, comb. nov. Basionym: *Warszewiczia obovata* Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 475. 1932.

Semaphyllanthe spectabilis (Steyerm.) L. Andersson, comb. nov. Basionym: *Calycophyllum spectabile* Steyerm., Mem. New York Bot. Gard. 10(5): 188. 1963.

Semaphyllanthe venezuelensis (Steyerm.) L. Andersson, comb. nov. Basionym: *Calycophyllum venezuelense* Steyerm., Mem. New York Bot. Gard. 10(5): 189. 1963.

Semaphyllanthe differs from *Calycophyllum* in having free (vs. calyptrate) stipules, plane (vs. saccate) bracteoles, a distinct tubular calyx (vs. one reduced to minute teeth), contorted (vs. imbricate) corolla aestivation, filaments inserted in center of corolla tube or lower (vs. at top), and filaments bristly hirsute toward base (vs. glabrous throughout). It is heavily centered on the Guiana shield and in the white sand campinas of the northern Amazon basin. Only the aberrant species *S. megistocaula* occurs outside of this area, in the southwestern Amazon. *Semaphyllanthe megistocaula* is included in the genus for practical reasons only: it shares the (plesiomorphic) diagnostic character states with the rest of the species, but is not reliably associated with them in the cladistic analysis.

Ferdinandusa Pohl, Pl. Bras. Icon. Descr. 2: 8. 1828. TYPE: Based on *Ferdinandea* Pohl.

Ferdinandea Pohl, Flora 10: 153. 1827, non *Ferdinanda* Lagasca. TYPE: Not designated.
Aspidanthera Benth., J. Bot. (Hooker) 3: 217. 1841.

TYPE: *Aspidanthera rudgeoides* Benth. = *Ferdinandusa rudgeoides* (Benth.) Wedd.
Gomphosia Wedd., Ann. Sci. Nat. Bot., Sér. 3, 10: 14. 1848. TYPE: Not designated.

Ferdinandusa is recognized by its free, contorted stipules, its more or less cochlear corolla lobes that are contorted in bud, its anthers with a dorsally widened and reinforced connective, its reticulate exine with two distinct size classes of lumina, and its large seeds. It is a neotropical genus heavily centered in the Amazon basin and is supposed to contain ca. 25 species (Andersson, 1992). It seems badly in need of a taxonomic revision, however.

Macrocnemum P. Browne, Civ. Nat. Hist. Jamaica 165. 1756. TYPE: *Macrocnemum jamaicense* L.

Lasionema D. Don, London Edinburgh Philos. Mag. & J. Sci. 2: 377. 1833. TYPE: *Lasionema roseum* (Ruiz López & Pavón) D. Don = *Cinchona rosea* Ruiz López & Pavón = *Macrocnemum roseum* (Ruiz López & Pavón) Wedd.

Macrocnemum is recognized by its reduplicate corolla lobes which are minutely hirtellous along the margins, its corolla tube which is minutely papillose inside below the filament attachments and which has linear thinnings running down from the sinuses to the filament bases, its loculicidal capsules, and its small seeds with the hilum located terminally or subterminally on the basiscopic wing. It is distributed in southern Central America, on Jamaica, and in subandean South America south to central Bolivia. In spite of its having ca. 14 presently recognized species (Andersson, 1992), the number of good species is probably less than half a dozen.

Tribe **Hillieae** Bremek. ex S. Darwin, Taxon 25: 603. 1976. TYPE: *Hillia* Jacq.

Trees or shrubs, rarely subshrubs, often epiphytic or chasmophytic. Raphides usually present (absent in *Blepharidium*). Stipules clasping to contorted in bud, or (usually) held flat back-to-back. Corolla lobes contorted or (*Blepharidium*) imbricate in bud; filaments short, glabrous, anthers linear, dorsifixed near middle or near base, or basifixed; ovary multiovulate, with distinct placentae attached to septum by a lamella, ovules ascendingly imbricate. Pollen 3-colporate, colpi with obtuse ends, os distinctly demarcated, or pollen 3-porate, exine reticulate, or foveolate to ± psilate. Fruit a usually septicidal capsule, apical portion (above calyx scar) prolonged and ± beaklike, calyx shed after anthesis. Seeds lenticular or planoconvex to ellipsoid,

with exotestal wing (rudimentary in *Hillia*), in *Hillia* also with long exotestal trichomes, hilum located centrally or marginally on seed body, exotesta cells with bandlike thickenings on inner tangential wall.

The tribe Hillieae is recognized mainly by its large woody capsules with the apical portion more or less prolonged and beaklike in mature fruit, and from which the calyx is shed soon after anthesis. The central core is formed by the genera *Balmea*, *Cosmibuena*, and *Hillia*. These are further characterized by the presence of raphides and contorted aestivation.

Hillia Jacq., Enum. Syst. Pl. 3. 1760. TYPE: *Hillia parasitica* Jacq.

Ravnia Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 49. 1852. *Hillia* subg. *Ravnia* (Oersted) C.M. Taylor, Selbyana 11: 30. 1989.

Hillia is characterized primarily by its rudimentary seed wing and presence of long exotestal hairs. It comprises 24 species distributed from southern Mexico through Central America and the West Indies to southern Brazil and Bolivia. The genus was monographed by Taylor (1994).

Cosmibuena Ruiz López & Pavón, Fl. Peruv. 3: 2. 1802, nom. cons., non *Cosmibuena* Ruiz López & Pavón, Fl. Peruv. Prodr. 10. 1794, nom. rejic. TYPE: *Cosmibuena obtusifolia* Ruiz López & Pavón, typus cons. = *Cosmibuena grandiflora* (Ruiz López & Pavón) Rusby = *Cinchona grandiflora* Ruiz López & Pavón.

Buena Pohl, Pl. Bras. Icon. Descr. 1: 8. 1826, non Cav. 1800. TYPE: *Cosmibuena grandiflora* (Ruiz López & Pavón) Rusby = *Cinchona grandiflora* Ruiz López & Pavón.

Cosmibuena is distinguished from *Hillia* by its stipules being fused intrapetiolarly at base, its well-developed seed wing, and the absence of exotestal trichomes. It comprises four species and is distributed from southern Mexico to central Bolivia and southeastern Brazil. It was revised by Taylor (1992). Some of the cladistic analyses performed by Taylor (1994) indicate that *Cosmibuena* may be paraphyletic when *Hillia* is separated.

Balmea Martínez, Bull. Torrey Bot. Club 69: 438. 1942. TYPE: *Balmea stormae* Martínez.

Balmea differs from *Cosmibuena* mainly in having free stipules, a cymose, many-flowered inflorescence, and a deep red to dark purplish corolla. It is a monotypic genus with the single species, *B.*

stormae, ranging from the state of Michoacán in central Mexico to northern Guatemala.

Blepharidium Standley, J. Wash. Acad. Sci. 8: 59. 1918. TYPE: *Blepharidium guatemalense* Standley.

Blepharidium agrees with other genera of the Hillieae in having large, woody capsules with a beaklike apical prolongation, and in having a caducous calyx. It differs from other members of the tribe in the absence of raphides, in having clasping stipules, corolla with imbricate aestivation, and anthers dorsifixed around the middle. It has been considered (Standley, 1940) to comprise two species, but *B. mexicanum* Standley is hardly specifically distinct from *B. guatemalense*. The genus is distributed from southern Mexico to northern Guatemala.

Tribe **Cinchoneae** DC., Ann. Mus. Natl. Hist. Nat. 9: 217. 1807, as "Cinchonaceae." TYPE: *Cinchona* L.

Trees or shrubs. Raphides absent. Stipules held flat back-to-back in bud, or (in species with verticillate leaves) held to form a cone and then marginally overlapping, free or intrapetiolarly fused at base, or calyptrate. Corolla lobes valvate in bud; filaments usually short or rather short, but often rather long in brevistylous morphs of heterostylous species, glabrous, anthers elongate to linear, dorsifixed near base; ovary multiovulate, with distinct placentae attached to septum by a lamella, ovules ascendingly imbricate. Pollen 3-colporate, colpi with obtuse to truncate ends, os poorly demarcated, exine foveolate. Fruit a septicidal capsule, apical portion not prolonged, calyx persistent. Seeds lenticular or planoconvex, with exotestal wing, hilum located centrally or marginally on seed body, exotesta cells with bandlike thickenings on inner tangential wall.

Pimentelia Wedd., Hist. Nat. Quinquinas 94. 1849. TYPE: *Pimentelia glomerata* Wedd.

Pimentelia is strongly reminiscent of *Stilpnophyllum* in having strongly "resinous" buds and young shoots, all inflorescences lateral, corolla strongly hairy inside in the upper part of the tube and all over the adaxial surface of the lobes, the hairs being coarse and thick-walled, and in having small capsules and small seeds. It differs, however, in having widely (vs. very narrowly) spaced lateral veins with a distinct tertiary venation in between.

Stilpnophyllum J. D. Hook., in Benth. & J. D. Hook., Gen. Pl. 2: 33. 1873. TYPE: *Stilpnophyllum lineatum* J. D. Hook.

Stilpnophyllum differs from *Pimentelia* mainly in leaf venation, having a large number (> 25 pairs) of fine, closely set secondary veins. It is a genus of four species (Andersson, 1994) distributed in the Andes of Ecuador and Peru.

Cinchonopsis L. Andersson, gen. nov. TYPE: *Cinchonopsis amazonica* (Standley) L. Andersson = *Cinchona amazonica* Standley.

A *Cinchona* differt flore parvo corolla alba campanulata tubo distali parte et lobis in tota superficiei grosse pubescentibus. A *Maguireocharide, Pimentelia,* et *Stilpnophyllo* differt praesentia inflorescentia terminali et capsula dehiscentia basifugi.

Trees. Leaves decussate; stipules interpetiolar, shortly fused across petiole at base, lingulate to triangular, held pressed back-to-back in bud, caducous. Inflorescences terminal and lateral, cymose. Flowers small, homostylous, normally 5-merous; calyx ± cup-shaped, with distinct lobes; corolla ± campanulate, white, tube ± equaling the lobes, or shorter, ± puberulous outside, densely bristly pubescent inside above stamen insertion, lobes valvate in bud, densely pubescent throughout on adaxial side with thick-walled hairs; stamens attached to corolla tube in central part, filaments ± equaling anthers, glabrous; anthers elongate, dorsifixed near base, with a small apical connective process, semi-exserted; stigma branches connivent. Capsules septicidal with acropetal dehiscence, crowned by the persistent calyx. Seeds winged, hilum located ± centrally on seed body, exotesta cells with bandlike, smooth secondary thickenings on inner tangential wall.

SPECIES INCLUDED:

Cinchonopsis amazonica (Standley) L. Andersson, comb. nov. Basionym: *Cinchona amazonica* Standley, Publ. Field Columbian Mus., Bot. Ser., 8: 334. 1931.

Standley (1931b) compared *Cinchona amazonica* to *C. micrantha* Ruiz López & Pavón and seems not to have been aware of the striking differences in floral structure between *C. amazonica* and other species of *Cinchona.* The decisive character for his placement of his new species was probably the acropetally dehiscent capsules. However, it differs from *Cinchona* in having small, homostylous flowers with a white, campanulate corolla, which is coarsely and densely pubescent inside in the distal part of the tube and throughout

the adaxial surface of the lobes, and in the absence of thinnings on the corolla tube. *Cinchonopsis* differs from *Maguireocharis, Pimentelia,* and *Stilpnophyllum* in having terminal inflorescences and acropetally dehiscent capsules. The only species seems to be widely distributed in the central and western Amazon basin and has been recorded from Peru, Colombia, Brazil (Amazonas and Roraima), and Venezuela.

Joosia Karsten, Fl. Columb. 1: 9. 1858. TYPE: *Joosia umbellifera* Karsten.

Joosia is recognized by its persistent stipules, the showy marginal appendages on the corolla lobes, fruits with valves that are usually deeply split loculicidally and with the halves often conspicuously coiled. The inflorescences are predominantly monochasial but this is sometimes not readily seen when they are congested into headlike clusters. *Joosia* is a genus of seven species (Andersson, 1994) distributed from Panama along the Andes to northern Bolivia; it is heavily centered in the Ecuadorean Andes.

Cinchona L., Sp. Pl. 172. 1753. Gen. Pl. ed. 5 79. 1754. TYPE: *Cinchona officinalis* L.

Kinkina Adans., Fam. Pl. 2: 147. 1763. TYPE: Based on *Cinchona* L.
Cinchona [sect.] *Quinquina* Endl., Gen. Pl. 556. 1838. TYPE: *Cinchona officinalis* L. (lectotype, designated by Andersson, 1994).

Cinchona is recognized, above all, by the marginally villose corolla lobes, the hairs of which are thin-walled and somewhat widened distally. It is further characterized by having terminal inflorescences, reddish (pink to purple) flowers, by the corolla lobes not being wedge-shaped at the apex and by the linear thinnings present in the corolla tube. The acropetal dehiscence of the capsule previously used to distinguish *Cinchona* on the one hand and *Ladenbergia* and *Remijia* on the other (e.g., Schumann, 1891), seems to be a constant feature of *Cinchona* but is not a reliable diagnostic feature; it occurs in *Cinchonopsis* and many species of *Remijia* and *Ladenbergia* as well. *Cinchona* is a genus of 20 to 25 species distributed from Costa Rica and the coastal mountains of Venezuela along the Andes to central Bolivia; it is heavily centered in the Andes of Ecuador and northern Peru.

Ladenbergia Klotzsch in Hayne, Getreue Darstell. Gew. 14: tab. 15. 1846. TYPE: *Ladenbergia moritziana* Klotzsch in Hayne (lectotype, designated by Andersson, 1994).

Cinchona [sect.] *Cascarilla* Endl., Gen. Pl. 556. 1838. *Cascarilla* (Endl.) Wedd., Ann. Sci. Nat. Bot., Sér. 3, 10: 10. 1849. TYPE: *Ladenbergia macrocarpa* (M. Vahl) Klotzsch in Hayne = *Cinchona macrocarpa* M. Vahl (lectotype, designated by Andersson, 1994).

Cascarilla [sect.] *Pseudoquina* Wedd., Hist. Nat. Quinquinas 79. 1849. TYPE: Not designated.

Cascarilla [sect.] *Carua* Wedd., Hist. Nat. Quinquinas 83. 1849. TYPE: *Cascarilla carua* Wedd. = *Ladenbergia carua* (Wedd.) Standley (lectotype, designated by Andersson, 1994).

Cascarilla [sect.] *Calyptrata* Wedd., Hist. Nat. Quinquinas 89. 1849. TYPE: *Cascarilla macrocarpa* (M. Vahl) Wedd. = *Cinchona macrocarpa* M. Vahl = *Ladenbergia macrocarpa* (M. Vahl) Klotzsch in Hayne (lectotype, designated by Andersson, 1994).

Cascarilla [sect.] *Muzonia* Wedd., Hist. Nat. Quinquinas 89. 1849. *Muzonia* (Wedd.) N. Osorio, Estudio Quinas Est. Unid. Colombia, ed. 2, 24. 1874. TYPE: *Cascarilla muzonensis* (Goudot) Wedd. = *Cinchona muzonensis* Goudot = *Ladenbergia muzonensis* (Goudot) Standley.

Ladenbergia is recognized by the presence of terminal inflorescences, white flowers, corolla lobes with a wedge-shaped terminal portion which is minutely papillose, and, usually, by large seeds ($\geq$ 11 mm long). It comprises ca. 40 species (Andersson, 1992) and has a wide distribution comprising southern Central America and most of humid tropical South America; it has conspicuous centers of diversity in the Guiana Highlands and the Northern Andes.

Remijia DC., Biblioth. Universelle Sci., Sci. Arts 41: 155. 1829. TYPE: *Remijia ferruginea* (A. St. Hil.) DC. = *Cinchona ferruginea* A. St. Hil. (lectotype, designated by Andersson, 1994).

Cephalodendron Steyerm., Mem. New York Bot. Gard. 23: 228. 1972. TYPE: *Cephalodendron globosum* Steyerm. (holotype).

Remijia is recognized by the absence of terminal inflorescences, usually thyrsiform inflorescences, white flowers, and by corolla lobes with the terminal part wedge-shaped and minutely papillose. It comprises ca. 40 presently recognized species (Andersson, 1992), but is partly in need of revision. It is widely distributed in tropical South America, but heavily centered on the western Guiana shield and adjacent parts of the Amazon basin.

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Appendix 1.   Representative material examined.

Alseis eggersii Standley: *Dodson & Gentry 12466* (SEL, US); *Eggers 15738* (S). *A. floribunda* Schott in Spreng.: *Hatschbach 46834* (GB); *Regnell III.1524* (S). *A. yucatanensis* Standley: *Contreras 950* (S); *Lundell 17955* (S). *Balmea stormae* Martínez: *Hinton 7894* (F, MO, US); *Rzedowski 34593* (NY). *Blepharidium guatemalense* Standley: *Contreras 9383* (S); *Jones & Facey 3433* (NY). *Calycophyllum candidissimum* (M. Vahl) DC.: *Budowski 33* (NY); *Bunting 8250* (NY). *C. intonsum* Steyerm.: *Berg et al. in Prance 19493* (S); *Prance 3738* (S). *C. megistocaulum* (Krause) C. M. Taylor: *Croat 20768* (AAU); *Ducke 24414* (S). *C. multiflorum* Griseb.: *Malme 1070B, 3006* (S). *C. obovatum* (Ducke) Ducke: *Clark & Maquirino 7656* (GB); *Ducke 266* (NY). *C. spruceanum* (Benth.) Hook. f.: *Holm-Nielsen et al. 21056* (AAU); *Krukoff 5416* (S). *C. venezuelense* Steyerm.: *Maguire et al. 46789* (NY). *Capirona decorticans* Spruce: *Mori & Bolten 8413* (S); *Palacios 3225* (GB). *Cephalodendron globosum* Steyerm.: *Maguire 42467* (NY); *Nee 31171* (NY). *Cinchona amazonica* Standley: *Fernández & Sanoja 4964* (NY); *Fosberg 38838* (NY). *C. barbacoensis* Karsten: *Pittier 517* (US); *van der Werff et al. 12028* (GB, MO). *C. calisaya* Wedd.: *Krukoff 11374* (NY), *Rusby 2347* (NY). *C. lancifolia* Mutis: *Fosberg 19570* (S), *20057* (US). *C. macrocalyx* Pav. ex DC.: *Madsen 75475, 86152* (AAU). *C. officinalis* L.: *Eriksson et al. 222* (GB); *Hart 762* (A). *C. pubescens* Vahl: *Harling & Andersson 22436* (GB); *Prieto AP-18* (S). *Cosmibuena grandiflora* (Ruiz López & Pavón) Rusby: *Maguire et al. 53574* (S); *Krukoff 10418* (S). *Dolicholobium oblongifolium* A. Gray: *A. C. Smith 5109, 7296* (S). *Ferdinandusa elliptica* Pohl: *Hatschbach 44786* (GB). *F. goudotiana* Schumann: *Tillett et al. 45184* (S). *F. uaupensis* Spruce ex Schumann: *Berry 2168* (NY), *Clark 7245* (NY). *Hillia parasitica* Jacq.: *Shafer 3297* (S); *Tollsten 141* (GB). *Hymenodictyon floribundum* (Hochst. & Steud.) Robinson: *"M. R." 22857* (NY); *Taylor 3399* (S). *Joosia aequatoria* Steyerm.: *Harling & Andersson 23643* (GB). *J. dichotoma* (Ruiz López & Pavón) Karsten: *Schunke 1100* (NY), *5442* (S). *J. dielseana* Standley: *Steere 8026* (NY); *Steyermark 54262* (F). *J. umbellifera* Karsten: *Grant 9983* (S); *von Sneidern 5005* (S). *Ladenbergia amazonensis* Ducke: *Williams 14493* (NY). *L. carua* (Wedd.) Standley: *Krukoff 11021* (NY); *Rusby G-1* (NY). *L. crassifolia* (DC.) Standley: *Camp E-4793* (NY), *Prieto AP-26B* (NY). *L. lambertiana* (C. Martius) Klotzsch in Hayne: *Maguire 32864* (NY); *Tillett & Tillett 45276* (NY). *L. macrocarpa* (Vahl) Klotzsch in Hayne: *Camp E-4322* (NY); *Jaramillo 9352* (AAU). *L. moritziana* Klotzsch in Hayne: *Steyermark 56925* (NY). *L. oblongifolia* (Mutis) L. Andersson: *Camp E-43* (NY), *E-55* (S). *L. pavonii* (Lambert) Standley: *Dodson & Gentry 9716* (F); *Gentry et al. 54751* (GB). *L. sericophylla* Standley: *Asplund 18914* (S); *Fosberg 22474* (NY). *L. undata* Klotzsch in Hayne: *Steyermark 56107, 56178* (NY). *Luculia intermedia* Hutch.: *Rock 7032* (S); *Tsai 55159* (S). *Macrocnemum cuencanum* Standley: *Prieto CP-14* (NY); *Steyermark 52709* (F). *M. jamaicense* L.: *Proctor 9999* (NY). *M. roseum* (Ruiz López & Pavón) Wedd.: *Palacios 2768* (GB); *Williams 5468* (S). *Maguireocharis neblinae* Steyerm.: *Maguire 37346* (NY). *Pimentelia glomerata* Wedd.: *Hodge 6017* (US); *Solomon 9290* (GB). *Remijia amazonica* Schumann: *Krukoff 7967* (S); *Prance et al. 4923* (S). *R. ferruginea* (A. St.-Hil.) DC.: *Regnell III.90* (S). *R. fir-*

mula (C. Martius) Wedd.: *Silva & Pinheiro 4207* (NY). *R. pacimonica* Standley: *Clark 6602* (NY). *R. pedunculata* (Karsten) Flückiger: *Fosberg & Fassett 21840* (S); *Jaramillo 6936* (GB). *R. pilosinervula* Steyerm.: *Pipoly et al. 7189* (NY); *Steyermark & Wurdack 713* (NY). *R. purdieana* Wedd.: *Fosberg & Fassett 21776* (NY). *R. vaupesiana* Steyerm.: *Fróes 21225* (NY). *Stilpnophyllum grandifolium* L. Andersson: *Neill & Palacios 9538* (MO); *Palacios et al. 8563* (GB). *S. oellgaardii* L. Andersson: *Oellgaard 74918* (AAU). *Wittmackanthus stanleyanus* (R. M. Schomb.) Kuntze: *Gentry et al. 19052* (MO).

Appendix 2.   Lists of apomorphies.

The two lists that follow use the following format: 7 3:1>>2 (0.500); 11:1>>3 [2](0.545). This should be interpreted thus: edge 7, character 3 transformed from state 1 to state 2 (consistency index 0.500); character 11 transformed from state 1 to state 3 [2 steps](consistency index 0.545). Double arrows (>>) indicate that the change is unambiguous, single arrows (>) that it is ambiguous. The number of steps is given only when distinct from 1. An asterisk indicates that this character was excluded during search in this particular run.

Figure 1A.—2 1:2>>1 (0.125). 4 16:1>>2 (0.250); 36:1>>2 (0.333); 60:2>>1 (0.500). 5 46:1>>2 (0.500). 7 3:1>>2 (0.500); 11:1>>3 [2](0.545); 16:1>>2 (0.250); 30:1>>3 [2](0.429); 31:2>>1 (0.500); 32:2>>1 (0.333); 41:2>>1 (0.200); 45:1>>3 (0.333); 50:1>>2 (0.091). 8 19:1>>2 (0.300); 27:2>>1 (0.500); 34:1>>2 (0.200); 50:1>>2 (0.091). 10 1:1>>2 (0.125). 12 21:2>>1 (0.857). 13 19:2>>1 (0.300). 14 1:2>>1 (0.125); 50:1>>2 (0.091). 15 1:2>>1 (0.125); 9:1>>5 (0.625); 16:1>>2 (0.250); 20:1>>3 (0.500); 27:2>>3 (0.500); 29:2>1 (0.333); 32:2>>1 (0.333); 38:2>>4 (0.571); 44:1>>2 (0.250); 50:1>>2 (0.091). 16 1:2>>1 (0.125); 11:2>>3 (0.545); 51:1>>2 (0.222). 17 1:2>>1 (0.200). 18 14:3>>1 (0.583). 19 19:1>>2 (0.300); 41:1>2 (0.200); 50:2>>1 (0.091). 20 4:1>>2 (0.400); 11:3>>4 (0.545); 14:3>>2 (0.583); 45:1>>3 (0.333); 52:1>>2 (0.750); 58:2>>3 (0.375). 21 1:2>>1 (0.125); 5:1>>2 (0.500); 17:2>>3 (0.571); 30:2>>1 (0.429); 41:1>2 (0.200); 55:2>>3 (0.800). 22 9:1>>2 (0.625); 21:1>>4 (0.857); 41:1>>2 (0.200); 44:1>>2 (0.250). 23 14:2>>3 (0.583); 22:1>>2 (1.000); *43:1>>2 (0.600); *47:1>>2 (0.667); 51:1>2 (0.222). 24 6:2>>1 (0.500); 58:2>>3 (0.375). 25 1:2>>1 (0.125). 26 *2:1>>2 (1.000); 5:1>>3 (0.500); 9:1>>4 (0.625). 27 *47:1>>3 (0.667). 28 9:1>>4 (0.625); 46:1>>2 (0.500). 29 6:1>>2 (0.500); *43:1>>2 (0.600); 51:1>2 (0.222). 30 6:1>>3 (0.500). 32 14:1>>4 (0.583). 33 19:1>>2 (0.300); 50:1>>2 (0.091). 34 41:2>3 (0.200). 35 4:1>>2 (0.400); 8:2>>1 (0.333); 36:1>>2 (0.333); 51:2>1 (0.222). 36 15:2>>3 (0.500); 34:1>>2 (0.200). 37 20:2>>1 (0.500). 38 4:1>>2 (0.400); 11:1>>2 (0.545); 14:1>>2 (0.583). 39 19:1>>2 (0.300); 20:2>>1 (0.500); 34:1>>2 (0.200). 40 4:1>>2 (0.400); 10:1>>3 (0.667); 14:1>>2 (0.583); 30:2>>3 (0.429); 58:2>>3 (0.375). 41 9:1>>6 (0.625); 11:3>>4 (0.545); 14:3>>5 (0.583); 30:2>>3 (0.429); *43:1>>2 (0.600); 45:1>>2 (0.333); 46:1>>3 (0.500). 42 9:1>>5 (0.625); 11:2>>1 (0.545); 17:2>>1 (0.571); 18:2>>3 (0.400); 19:1>>2 (0.300); 33:1>>2 (0.500); 34:1>>2

(0.200); 38:2>>4 (0.571); 40:1>>3 (0.333); 41:1>3 (0.200); 45:1>>3 (0.333). 45 28:2>>1 (0.667); 30: 2>>1 (0.429); 31:1>>2 (0.500); 32:1>>2 (0.333); 41:1>2 (0.200); 42:2>>1 (0.500); 44:2>>1 (0.250); 58:2>>1 (0.375). 46 21:1>>2 (0.857); 29:1>2 (0.333); 46:1>2 (0.500). 47 11:2>>1 (0.545); 18: 2>1 (0.400); 38:2>1 (0.571); 60:1>>2 (0.500). 48 9:1>>5 (0.625); 13: 1>>2 (1.000); 17:2>>4 (0.571); 18:1>3 (0.400); 27:2>>1 (0.500); 37:1>>2 (1.000); 38:1>3 (0.571); 39:1>>2 (1.000); 45:1>>3 (0.333). 49 58:1>>2 (0.375). 50 1:2>>1 (0.125); 14:3>>2 (0.583); 46:2>1 (0.500). 51 4:1>>3 [2](0.400); 6:1>>2 (0.500); 15:2>4 (0.500). 52 10:1>>2 (0.667); 14:2>>6 (0.583); 17:2>>3 (0.571); 27:2>>3 (0.500); 29:2>>1 (0.333). 53 6:2>>3 (0.500); 38:1>>3 (0.571); 58:1>>2 (0.375). 54 14:2>>1 (0.583); 16: 1>>2 (0.250). 55 *47:1>>2 (0.667); 51:1>>2 (0.222). 56 4:1>>2 (0.400); 17:2>3 (0.571); 19:1>>2 (0.300); 48:2>>1 (0.714); 55:1>>2 (0.800). 57 5:2>>1 (0.500); 14:3>>2 (0.583); 17:3>5 (0.571); 22:1>>3 (1.000); 23:1>>2 (0.500); 24:1>>2 (0.750); 40:1>>3 (0.333); 41:2>>3 (0.200); 45:1>>3 (0.333); 58:1>>2 (0.375); 59:1>>2 (0.667). 58 8:1>>2 (0.333). 59 15:2>>1 (0.500); 35:1>>2 (1.000); 48: 2>>3 (0.714); 56:1>>2 (1.000). 60 5:2>>1 (0.500); 11:2>>3 (0.545); 27:2>>3 (0.500); 49:1>2 (0.500); 50:1>>2 (0.091); 53:1>>2 (1.000). 61 55:1>>2 (0.800). 62 15:2>3 (0.500); 33:1>>2 (0.500). 63 8:1>>2 (0.333); 14:3>1 (0.583); 38:2>>1 (0.571); 49:2>1 (0.500); 52:1>3 (0.750). 64 20:1>>2 (0.500); 27:3>>2 (0.500); 42:2>>1 (0.500); 44:2>>1 (0.250). 65 11:3>>2 (0.545); 17:2>>1 (0.571); 40:1>2 (0.333); 50:2>1 (0.091); 51:1>2 (0.222); 52:3>1 (0.750); 54:1>>2 (1.000). 66 12:1>>2 (1.000). 67 24:1>>2 (0.750); 25:1>>2 (1.000). 68 4:1>2 (0.400); 14:1>>2 (0.583); 40:2>1 (0.333). 69 6:1>>2 (0.500). 70 50:1>>2 (0.091). 71 8:2>>1 (0.333); 48:2>>3 (0.714); 51:2>1 (0.222). 72 11:2>>4 [2](0.545). 73 8:2>>1 (0.333); 15:2>3 (0.500); 51:2>1 (0.222). 74 19:1>>2 (0.300); 23:1>>2 (0.500); 24:1>>3 (0.750); 28:2>>3 (0.667). 75 50:1>>2 (0.091). 76 3:1>>2 (0.500); 9:1>>3 (0.625); 10:1>>3 (0.667); 26:1>>2 (1.000); 36:1>>2 (0.333); 40:2>1 (0.333); 41:1>2 (0.200); 59:1>2 (0.667). 77 34:1>>2 (0.200); 59: 2>3 (0.667). 78 14:1>3 (0.583); 21:1>>3 (0.857); 24:1>>4 (0.750). 79 6:1>>2 (0.500); 11:2>>1 (0.545); 18:2>1 (0.400); 50:1>2 (0.091). 80 14:3>1 (0.583); 28:2>>1 (0.667); 40:2>1 (0.333). 81 7:1>>2 (1.000); 18:1>2 (0.400); 48:2>>1 (0.714); *57:1>2 (1.000).

Figure 2A.—1 *14:2>3 (0.517); 19:1>>2 (0.375); 50:2>>1 (0.273). 2 4:1>>2 (0.375); 45:2>3 (0.667); 52:1>>2 (0.667). 3 9:1>>6 (1.000); *14:2>5 (0.517); *33:2>1 (0.500); 43:1>>2 (0.500); *46:1>>3 (0.667); 55:2>>1 (0.857). 4 1:2>1 (0.250); 5:1>>2 (0.667); 7:2>>3 (1.000); 30:2>1 (0.600); 52:1>>3 (0.667); 55:2>>3 (0.857). 5 9:4>>2 (1.000); *14: 1>>2 (0.517); 21:1>>4 (1.000); 41:1>>2 (0.286); 44:1>>2 (0.500). 6 8:1>>2 (0.600). 7 40:1>>2 (0.333); *46:1>>2 (0.667). 9 4:1>>3 [2](0.375); 50: 2>>1 (0.273). 10 43:1>>2 (0.500). 11 51:2>>1 (0.200); 58:2>>3 (0.375). 12 4:1>>2 (0.375); 50:

2>>1 (0.273). 13 *14:1>>3 (0.517). 14 1:2>>1 (0.250). 15 58:2>>3 (0.375). 16 *14:1>>2 (0.517); 15:2>>4 (0.429); 40:1>>2 (0.333). 17 *14:1>>2 (0.517); 58:2>>3 (0.375). 18 6:1>2 (0.600); 57:1>>2 (0.333). 20 58:2>>3 (0.375). 21 *14:1>>3 (0.517); 22:1>>2 (0.750). 22 51:2>1 (0.200). 23 37:1>>2 (1.000). 24 1:2>>1 (0.250). 25 *14:1>>2 (0.517); 48:2>>3 (0.692). 26 36:1>>2 (0.500). 28 *14:1>>2 (0.517). 29 43:1>>2 (0.500). 31 11:2>>3 (0.739). 32 *14:1>>4 (0.517). 33 34:1>>2 (0.250). 34 34: 1>>2 (0.250); *59:2>3 (0.667). 35 4:1>>2 (0.375); 8:2>>1 (0.333); *14:1>3 (0.517); 28:1>2 (0.500); 36:1>>2 (0.500); 40:1>>2 (0.333); 51:2>>1 (0.200). 36 34:1>>2 (0.250). 37 20:2>>1 (0.333). 38 4:1>>2 (0.375); 11:1>2 (0.739); *14:1>2 (0.517). 39 *14: 1>3 (0.517); 19:1>>2 (0.375); 20:2>>1 (0.333); 34: 1>>2 (0.250); 40:1>>2 (0.333); 50:2>>1 (0.273). 40 4:1>>2 (0.375); 10:1>>3 (0.500); *14:1>2 (0.517); 30:2>>3 (0.600); 52:1>>3 (0.667); 58:2>>3 (0.375). 41 5:1>>2 (0.667); 8:2>>1 (0.333); *14: 1>3 (0.517); *35:1>>2 (1.000); 48:2>>3 (0.692); 50:2>>1 (0.273); 51:1>>2 (0.200); *56:1>>2 (1.000); 58:2>>1 (0.375). 42 4:1>>2 (0.375); 11: 3>>2 (0.739); 17:2>>5 (1.000); 19:1>>2 (0.375); 22:1>>3 (0.750); 23:1>>2 (0.500); 24:1>>2 (0.750); *29: (1.000); 40:1>>3 (0.333); 41:2>>3 (0.286); 45: 1>>3 (0.667); *46:1>>2 (0.667); 48:2>>1 (0.692); *59:1>>2 (0.667). 44 1:1>2 (0.250); 15:1>2 (0.429); 28:1>>2 (0.500); 30:1>2 (0.600); *31:2>>1 (1.000); *32:2>>1 (1.000); 38:2>1 (0.600); 53:1>>2 (1.000); 55:1>2 (0.857). 45 27:2>>3 (1.000); 42:1>>2 (1.000); 44:1>>2 (0.500). 46 8:2>>1 (0.333); *14: 1>2 (0.517); 15:2>3 (0.429); *33:1>2 (0.500); 38: 1>2 (0.600); 49:1>>2 (1.000). 47 11:3>>4 (0.739); 30:2>3 (0.600); 41:2>>1 (0.286); 45:1>2 (0.667); 58:2>3 (0.375). 48 20:1>>2 (0.333); 41:2>>1 (0.286). 49 1:3>>2 (0.739); 17:2>>1 (1.000); 54: 1>>2 (1.000). 50 8:2>1 (0.333); 12:1>>2 (1.000). 51 6:1>>2 (0.600); 24:1>>2 (0.750); 25:1>>2 (1.000). 52 8:1>2 (0.333); 51:1>>2 (0.200). 53 9:1>>4 (1.000). 54 6:2>>1 (0.600); 50:2>>1 (0.273). 55 19:1>2 (0.375). 56 2:1>>2 (1.000); 5:1>>3 (0.667); *14:1>>2 (0.517); 15:2>3 (0.429). 57 11:2>3 (0.739); 41:1>>2 (0.286). 58 37:1>>3 (1.000); 48:2>>3 (0.692). 59 47:1>>3 (1.000). 60 4:1>>2 (0.375); 48:2>>3 (0.692). 61 11:2>>3 (0.739). 62 6:2>1 (0.600). 63 50:2>>1 (0.273). 64 4:2>1 (0.375); 22:1>>2 (0.750); 51:1>>2 (0.200). 65 11:3>>4 (0.739). 66 43:1>>2 (0.500); 51:1>2 (0.200). 67 47:1>>2 (1.000). 68 4:2>>1 (0.375); 6:2>>1 (0.600). 69 4:2>>3 (0.375); *14:1>2 (0.517). 15:2>>1 (0.429); 22:1>>4 (0.750); 57:1>>2 (0.333). 70 15:2>3 (0.429); 19:1>>2 (0.375). 71 23:1>>2 (0.500); 24:1>>3 (0.750); 28:2>>3 (0.500); 40:1>>2 (0.333). 72 6:1>>3 (0.600). 73 6:1>2 (0.600); 50: 2>>1 (0.273); 51:1>>2 (0.200). 74 3:1>>2 (1.000); 9:1>>3 (1.000); 10:1>>3 (0.500); 26:1>>2 (1.000); 36:1>>2 (0.500); 41:1>2 (0.286); *59:1>2 (0.667). 75 41:2>3 (0.286). 76 19:2>>1 (0.375); 50:2>>1 (0.273). 77 21:1>>3 (1.000); 24:1>>4 (0.750); 51: 1>>2 (0.200). 78 6:1>>2 (0.600); 11:2>1 (0.739); 28:2>1 (0.500). 79 15:2>3 (0.429); 18:2>>1 (1.000). 80 7:1>>2 (1.000); 48:2>>1 (0.692); 57:1>2 (0.333).